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Vision Research

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Foveal color perception: Minimal thresholds at a boundary between perceptual categories

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ARTICLE INFO

Article history:

Received 20 July 2011

Received in revised form 6 April 2012

Available online 19 April 2012

Keywords:

Color discrimination

Color appearance

Color category

Unique hue

Color opponent channel

Categorical perception

Category boundary

ABSTRACT

Human color vision depends on the relative rates at which photons are absorbed by the three classes of retinal cone cell. The ratios of these cone absorptions can be represented in a continuous two-dimensional space, but human perception imposes discrete hue categories on this space. We ask whether discrimination is enhanced at the boundary between color categories, as it is at the boundary between speech sounds. Measuring foveal color discrimination under neutral conditions of adaptation, we find a region of enhanced discrimination in color space that corresponds approximately to the subjective category boundary between reddish and greenish hues. We suggest that these chromaticities are ones at which an opponent neural channel is in equilibrium. This channel would be 'non-cardinal', in that its signals would not correspond to either axis of the MacLeod–Boynton chromaticity diagram.

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1. Introduction

Human color vision depends on three types of retinal cone that have their maximal sensitivities in different parts of the visible spectrum (Smith & Pokorny, 2003). To identify colors, the visual system compares the rates at which photons are being absorbed in the three classes of cone within a given local region of the receptor array (Rushton, 1972). So in principle, given three independent and univariant signals, all chromatic stimuli can be represented by two ratios, as in the MacLeod–Boynton (1979) chromaticity diagram (Fig. 1A).

1.1. Color categories and neural signals

The chromaticity diagram varies continuously in two dimensions. Yet human perception imposes discrete categories upon this continuous space, so that our perceptual experience is of a limited number of distinct hues. If viewing conditions are confined to isolated lights and if adaptation is neutral, most observers identify four *Urfarben* or 'unique hues': red, green, yellow and blue, plus white and black; and judge that in other hues, such as orange or cyan, they can subjectively discern more than one of the *Urfarben* (Hering, 1878; Shevell, 2003; Sternheim & Boynton, 1966; Webster et al., 2002).

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It remains uncertain whether there are neural categories – neural structures or signals – that are coincident with the phenomenological categories (Mollon & Jordan, 1997). Certainly, according to a conventional view, the phenomenological categories do not map onto the signals of the two types of color-opponent neuron that are thought to carry color information at early stages of the primate visual system. One of these neural signals represents the difference, or ratio, of the long- (*L*) and middle-wave (*M*) cone excitations; and it is carried by the midget ganglion cells of the retina and by the parvocellular units of the LGN (Dacey, 2003; Derrington, Krauskopf, & Lennie, 1984; Gouras, 1968). The other opponent signal represents the ratio of short-wave (*S*) cone excitations to a combined *L* and *M* signal; it is carried by the small bistratified ganglion cells and by units in koniocellular laminae 3 and 4 of the LGN (Dacey & Lee, 1994). The signals of these two neural channels correspond respectively to the horizontal and the vertical axes of the MacLeod–Boynton diagram (Fig. 1A). In a psychophysical context, the two axes are often termed the 'cardinal' directions of color space, a usage introduced by Krauskopf, Williams, and Heeley (1982).

When the observer is in a neutral state of adaptation, the chromaticity space of Fig. 1A is divided into reddish and greenish hues by a line that runs from the wavelength of pure, or 'unique', blue (~475 nm) to the wavelength of unique yellow (~575 nm) (Jordan & Mollon, 1997; Kuehni, 2004; Nerger, Volbrecht, & Ayde, 1995). This category boundary, however, lies obliquely in the diagram and is not aligned with either axis. In other words – and this is the fundamental mystery – the perceptual category boundary does not correspond to a constant excitation of either one of the

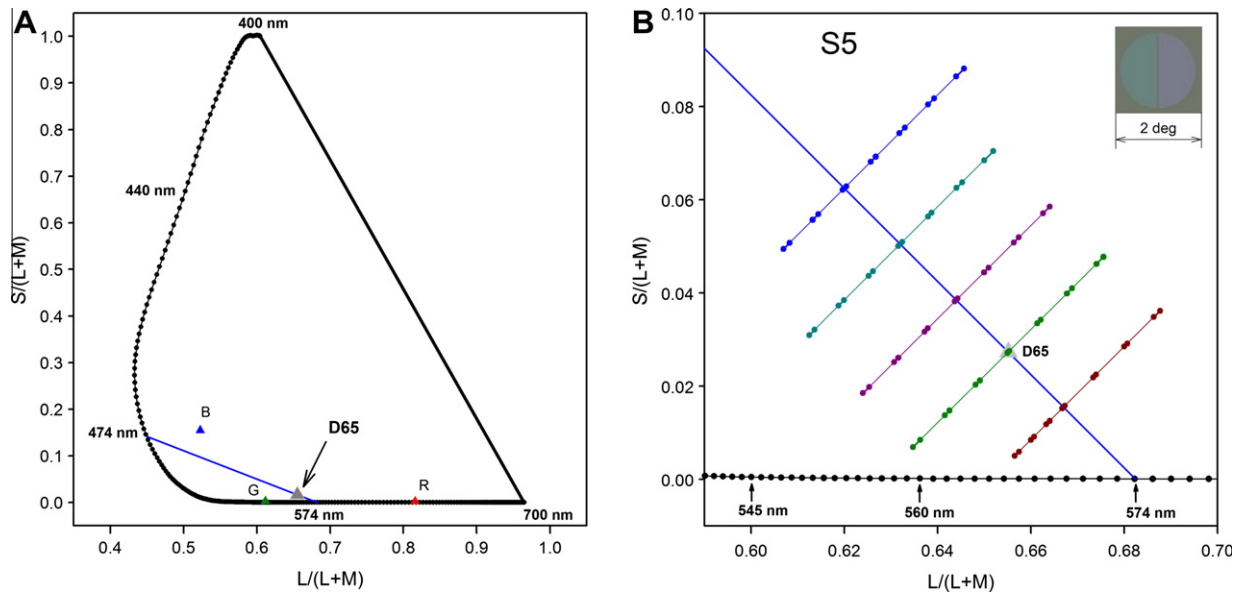


Fig. 1. (A) The MacLeod–Boynton (1979) chromaticity diagram. The axes of this diagram correspond to two chromatically opponent neural channels that have been identified in the primate visual system. The ordinate represents the signal $S/(L + M)$, a signal extracted by the small bistratified ganglion cells of the retina; and the abscissa represents the signal $L/(L + M)$, a signal extracted by the midsize ganglion cells. The symbols R, G, B indicate the chromaticities of the phosphors of our monitors. The locus of hues that are subjectively neither reddish nor greenish (the ‘blue–yellow’ line) runs obliquely in the diagram and is not aligned with either axis. ‘D65’ identifies the chromaticity of the standard daylight illuminant and this chromaticity was used for the background in our experiments. (B) A magnified plot of the MacLeod–Boynton diagram, with the ordinate scaled so that the yellow–blue line lies at -45° . We measured hue discrimination along the five lines orthogonal to this line. At seven positions on each line the separation of the paired points shows directly the threshold for this observer. The set of connected filled circles at the base of the diagram represents part of the spectrum locus. *Inset*: the spatial arrangement of the two half fields to be discriminated.

chromatically-opponent neural channels thought to be present at early stages of the visual system. In some models of color vision (e.g. De Valois & De Valois, 1993), a rearrangement of the LGN channels is postulated to give cortical substrates or signals that do correspond to the phenomenological axes; but the location and nature of these substrates or signals – as well as their very existence – remain uncertain (Mollon, 2009; Webster et al., 2002).

1.2. Discrimination at a category boundary

In the case of speech perception, discrimination is enhanced at the boundaries between phonemes, such as the boundaries between the voiced stops *b*, *d* and *g* (Liberman et al., 1957). Does a similar enhancement of discrimination occur at boundaries between phenomenological color categories?

Several recent studies have measured the speed of discrimination at category boundaries between hues. For example, Witzel, Hansen, and Gegenfurtner (2009) equated stimuli for discriminability in a threshold task and found that reaction times were shorter for discriminating colors that straddled the blue–green boundary than for discriminating colors lying within one or the other category. Moreover, there is evidence that linguistic categories may influence perceptual categories. Winawer et al. (2007), using a series of blue stimuli, have shown that native Russian speakers respond more rapidly when the target and distractor colors lie on opposite sides of the boundary between *goluboy* and *sinii*. (For a Russian speaker, these two categories differ in hue and lightness and there is no general word for ‘blue’.) Native speakers of English did not enjoy a comparable advantage at the boundary between ‘light blue’ and ‘dark blue’. Roberson and colleagues have reported a similar difference between English and Korean speakers at the boundary that Korean marks between yellow–green and green (Roberson, Pak, & Hanley, 2008). The effect of linguistic categories may be especially strong when the stimuli are presented in the right visual field (Franklin et al., 2008; Gilbert et al., 2006);

and this effect may be found even when the categories are learnt in the laboratory in adulthood (Zhou et al., 2010).

However, in all these studies the dependent variable is speed and it is possible that the category effects occur at a response stage (Roberson, Hanley, & Pak, 2009; Zhou et al., 2010). Is the actual precision of discrimination also enhanced at a boundary between color categories – as has been found in the case of speech perception? In a recent study (Danilova & Mollon, 2010), using a forced-choice, performance method, we measured color discrimination thresholds for spatially separated targets presented in the parafovea at an eccentricity of 5° of visual angle. We found that discrimination was enhanced near the category boundary between reddish and greenish colors. That study was conceived within the context of our earlier work on comparison of stimuli that are separated in the visual field (Danilova & Mollon, 2003, 2006). It might be supposed that we were dealing with a special case, where the colors of the two stimuli were categorized before being compared; in other words, two independent signals might be extracted in the early visual system and they might be compared only at a central level where the representations were categorical. In the present study, we use juxtaposed stimuli arranged as two foveal half-fields – a more conventional configuration for studying the limits of color discrimination.

We measure discrimination not at the transition between two primary hues of the color circle (such as the transition between blue and green), but at a unique hue, where there is a transition, say, from greenish blues to reddish blues. Our measurements are made at a number of points along lines orthogonal to the yellow–blue line of Fig 1A. We find that the points of optimal discrimination fall on an oblique locus in the MacLeod–Boynton chromaticity diagram and are approximately aligned with the subjective category boundary between reddish and greenish hues – the line defined by unique blues, unique yellows and white. (We follow Burns et al. (1984) in extending the terms ‘unique blue’ and ‘unique yellow’ to include not only monochromatic lights but

also lights in the interior of color space that appear neither reddish nor greenish.)

In any study of discrimination at category boundaries, it is essential to express thresholds in an independent metric. To use, say, the Munsell system would be inappropriate, since the Munsell samples were developed to be approximately equally separated in perceptual space. Here we express thresholds in terms of the change required in the ratio of cone excitations in order to support a criterion level of discrimination.

2. Experiment 1. Methods

2.1. Apparatus and stimuli

Measurements were made in St. Petersburg, Russia, and in Cambridge, England, using calibrated Mitsubishi color monitors (Diamond Pro 2070) and Cambridge Research Systems graphics boards (ViSaGe in St. Petersburg, VSG2/3 in Cambridge). In St. Petersburg, the display had a refresh rate of 80 Hz and a resolution of 1280×980 pixels; in Cambridge, these values were 92 Hz and 1024×768 pixels. Calibration procedures and algorithms for generating colors on the CRT screen were identical in the two laboratories. The ViSaGe system allowed a resolution of 14 bits per gun, the VSG system, 15 bits. We checked that our measured thresholds were not instrumentally limited.

To specify the colors of stimuli we used the MacLeod–Boynton diagram (Fig. 1), constructing it from the cone sensitivities tabulated by DeMarco, Pokorny, and Smith (1992). The plane of the diagram is a plane of equal luminance for the Judd₍₁₉₅₁₎ observer. Luminance is equivalent to the sum of the *L*- and *M*-cone signals, $L + M$ (Smith & Pokorny, 1975). Our provisional yellow–blue line was based on pilot settings by the two authors using the procedure described below (§2.2). We rescaled the vertical ordinate of the MacLeod–Boynton diagram so that this yellow–blue line lay at -45° . The provisional line passes through the chromaticities of CIE Illuminant D65 and of a monochromatic light of 574 nm. Our stimuli are not critically dependent on the use of the DeMarco et al. fundamentals: Fig. 1B has an almost identical appearance when the MacLeod–Boynton diagram is reconstructed with the fundamentals of Stockman and Sharpe (2000).

The targets were presented on a steady background metameric to the daylight illuminant D65 (Wyszecki & Stiles, 1982). The luminance of the background was set to have a value equivalent to 10 cd m^{-2} in CIE units. The circular bipartite target field subtended 2 deg and was vertically divided by a thin line that had the chromaticity and luminance of the background (Fig. 1B inset). The target half-fields had a mean luminance that was 30% greater than that of the background when expressed in the $(L + M)$ units of our space; but to ensure that the observers could not discriminate the stimuli on the basis of differences in sensation luminance, we jittered independently the $(L + M)$ value of each target. The range of jitter was $\pm 5\%$ of the mean value in Experiments 1 and 2, but was reduced to $\pm 1\%$ in Experiment 3 in view of the small size of the chromatic thresholds obtained in Experiment 1. The duration of the target was 150 ms.

The CRT screen was viewed binocularly from a distance of 570 mm. To maintain central fixation, a diamond array of small black dots surrounded the region in which the target field was presented.

2.2. Procedures

In Experiment 1, in any given experimental session, we tested discrimination along one of the five $+45^\circ$ lines shown in Fig. 1B. The task was a spatial forced choice. Formally the observer's task

was to indicate by pushbuttons which stimulus hemifield had the lower $L/(L + M)$ value: informally, the target half-field could often be identified as 'greener' (or 'less red'), but the task was a performance one, and auditory feedback on each trial told the observer what was the correct response. Within one experimental session, thresholds were measured around seven different 'reference' points on one of the $+45^\circ$ lines, in random order. The reference chromaticity was never itself presented, but any given pair of discriminanda lay on the same line, straddling the reference point; and their chromatic separation was increased or decreased symmetrically around the reference chromaticity according to the observer's accuracy. Since the subjective appearance of the stimuli varied greatly at different reference positions and since we wished to minimize any central tendencies within the set of seven reference stimuli, we tested only one reference stimulus in a given block of trials, to allow the observer to take full advantage of the auditory feedback. For these performance measurements, where the correct answer on each trial is independent of the preceding, we used a single staircase, which terminated after 15 reversals; the last 10 reversal points were averaged to give a threshold. The staircase tracked 79.4% correct (Wetherill & Levitt, 1965). The reference and test chromaticities were expressed in terms of the abscissa of the chromaticity diagram (i.e. their $L/(L + M)$ or *l* coordinate) and the corresponding $S/(L + M)$ coordinate was then calculated so that they lay on the same 45° line. At any one point on the staircase, one of the discriminanda had an *l* coordinate l_{t1} and the other had an *l* coordinate l_{t2} , where l_{t1} was equivalent to the reference coordinate l_r multiplied by a factor *a*, and l_{t2} was equivalent to l_r divided by *a*, where *a* is always >1.0 . The starting value of *a* was 1.001; after three correct responses, the value $(a - 1)$ was reduced by 10% and after each incorrect response it was increased by 10%.

The different 45° lines were tested in randomized order; and six repetitions were performed for each 45° line, the first being treated as practice and not included in the analysis.

Interleaved with the threshold measurements, there were also six independent experimental sessions in which we estimated the subjective red–green transition point, the first session being discarded as practice. For these phenomenological measurements a uniform 2-deg disk was presented for 150 ms on the standard white background. In individual blocks of trials within one experimental session, the chromaticity of the disk was varied along one of the $+45^\circ$ lines of Fig. 1B, and the subject was asked to indicate by pushbuttons whether the target appeared reddish or greenish. To avoid sequential effects in the phenomenological measurements, four randomly interleaved staircases were used to estimate the transition point between reddish and greenish hues, two staircases starting on each side of the expected match (Jordan & Mollon, 1995). Each staircase terminated after 15 reversals. The last 10 reversals of each of the 4 staircases were pooled to give an estimate of the unique hue for a given line. In any one experimental session, the perceptual transition points were estimated for all five of the $+45^\circ$ lines of Fig. 1B, in a different random order in different sessions. The same method was used in a pilot study to obtain the initial scaling of the MacLeod–Boynton diagram.

2.3. Observers

All observers had normal color vision as tested by the Cambridge Colour Test (Regan, Reffin, & Mollon, 1994). Observers 1 and 2 were the authors JDM and MVD respectively; the other subjects were psychophysically practiced but were naïve as to the purpose of the experiments. Observers 2, 3 and 5 are female. Observers 2–4 are native Russian speakers, whereas 1 and 5 are native English speakers. All observers except observer 5 were tested in St. Petersburg. The experiments in both Cambridge and St.

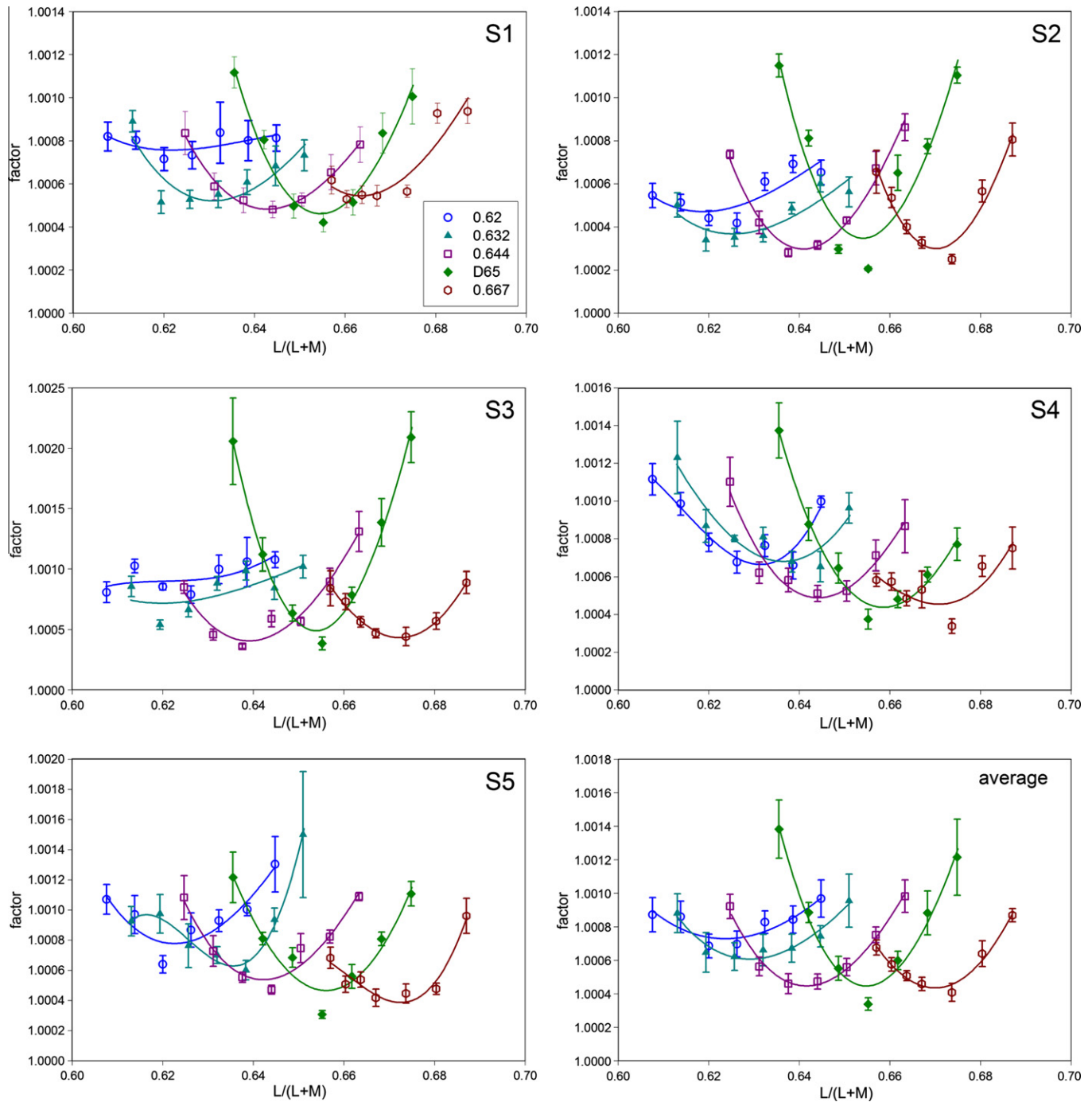


Fig. 2. Color discrimination results for five subjects; the last panel shows averages. Within each panel, each data set represented by different symbols corresponds to one of the five $+45^\circ$ lines in Fig. 1B. The ordinate represents the factor by which each of the discriminanda differs from the referent at threshold. These thresholds are plotted against the $L/(L+M)$ coordinate of the referent. The functions fitted to the data sets are inverse third-order polynomials; they have no theoretical significance but are used to derive the minima plotted in Fig. 3. Note that the minima do not occur at a constant value of $L/(L+M)$. In the first five panels, the error bars represent ± 1 SEM, based on estimates from five independent experimental sessions for individual observers; in the final panel (average data) they are based on the five mean values from the different observers.

Petersburg were approved by the Psychology Research Ethics Committee of the University of Cambridge.

3. Experiment 1. Results

A very direct representation of the discrimination thresholds can be seen for one observer in Fig. 1B, which represents a magnified region of the MacLeod–Boynton chromaticity diagram: Each pair of data points, linked by a short line, represents a pair of chromaticities that were discriminable on 79.4% of trials. Notice that the separation of the linked targets varies along each line. The minimal separation is typically in the middle of each range and neither the $L/(L+M)$ coordinate nor the $S/(L+M)$ coordinate of the minimal threshold is constant between the different $+45^\circ$ lines.

Fig. 2 shows the discrimination thresholds for all 5 of our observers. In this way of plotting the thresholds, the abscissa shows the $L/(L+M)$ coordinate at which each threshold was measured, and the ordinate shows the factor by which the $L/(L+M)$ values of the two half fields must differ in opposite directions.

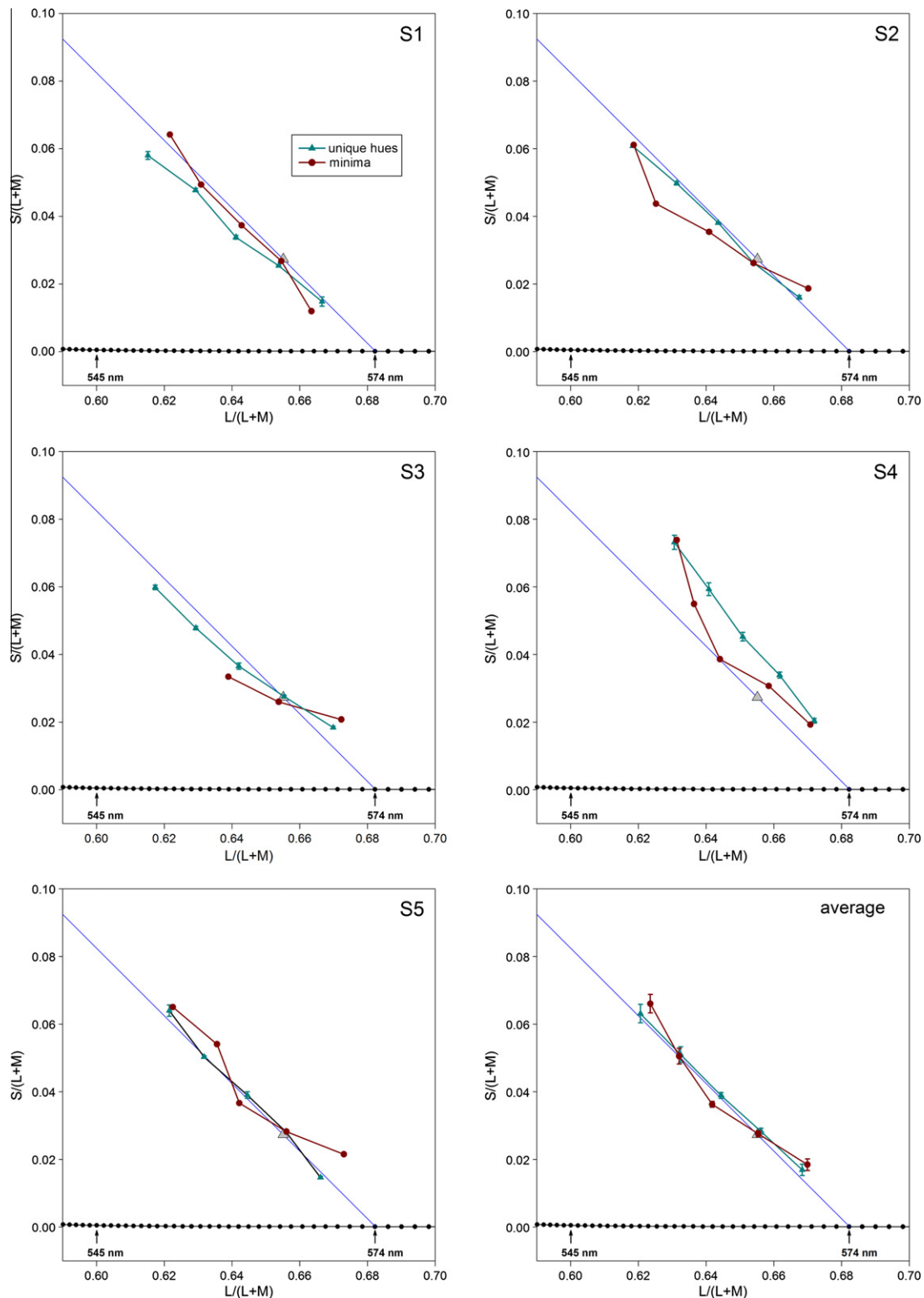


Fig. 3. The first five panels show for individual observers the chromaticities that correspond to the subjective red–green category boundary, i.e. colors that are ‘unique blue’ or white or ‘unique yellow’ (triangles). Also shown are the minimal discrimination thresholds for equivalent conditions (circles). These minima are derived from the fits of Fig. 2. Observer 3 did not show clear performance minima for two conditions (see Fig. 2). The sixth panel shows average results. Error bars for the phenomenological judgements are ± 1 SEM (based on five independent runs in the case of individual observers; and on the 5 individual means in the case of the average.) No error bars are shown for the performance measurements for individual observers, since these are derived from the fits of Fig. 2; but ± 1 SEM is shown for the average for the five observers. Where no error bar is visible, the SEM is smaller than the symbol.

tions from the reference point if they are to be correctly discriminated on 79.4% of presentations. Within each panel, different subsets of data correspond to the different $+45^\circ$ lines in Fig. 1B. The

observers all show a similar pattern of results: For each subset of thresholds, corresponding to one $+45^\circ$ line, there is usually a clear minimum, but the minima occur at different $L/(L+M)$ coordinates

for different lines. If the lowest thresholds always coincided with the equilibrium point of a neural channel that extracted the ratio of L and M excitations (the signal traditionally attributed to the mid-ganglion cells of the retina), then the minima should all coincide with the same value of $L/(L+M)$, the value corresponding to that of the D65 background. This is clearly not the case. Nor do the minima all coincide with the same value of $S/(L+M)$, as would be expected if discrimination depended on the signal traditionally associated with the small bistratified ganglion cells. These results for conventional foveal targets confirm our earlier findings, obtained while studying the discrimination of spatially separated colors in parafoveal vision (Danilova & Mollon, 2010).

For most subjects, the minima in the threshold functions are most marked for the $+45^\circ$ lines closest to D65. The minima become less marked when $S/(L+M)$ values are high and $L/(L+M)$ values are low. This has been our consistent finding in pilot studies.

In experimental runs interleaved with the threshold measurements, we also estimated the locus of the subjective yellow–blue line for each observer. In these phenomenological measurements, the observer judged whether a 2-deg disk was reddish or greenish (see §2.2). In Fig. 3, we plot, for each subject and for each of the $+45^\circ$ lines, the chromaticities judged to be neither reddish nor greenish, i.e. colors that lie on the yellow–blue line. We also plot the performance minima, estimated from the fits to the forced-choice data of Fig. 2. In most cases the performance minima lie close to the subjective category boundary between reddish and greenish colors. In Section 10, we interpret these minima as corresponding to the equilibrium point of a chromatic channel that is not aligned with either of the axes of the MacLeod–Boynton diagram – a channel that is instead aligned with the red–green dimension of subjective color space.

4. Experiment 2. Control for bias in the set of referents

For the three central $+45^\circ$ lines probed in Experiment 1, the average chromaticity of the set of referents coincides approximately with the point of red–green equilibrium (see Fig. 1B). These are lines for which most observers show a clear minimum in thresholds. In contrast, the set of referents chosen for the leftmost $+45^\circ$ line (which intersects the original yellow–blue line at an $L/(L+M)$ coordinate of 0.62) is necessarily asymmetric, owing to limitations imposed by the monitor gamut; and this is the line that gives the poorest minimum in the thresholds. Is this coincidence or could our results depend on the particular range of referents that we used? Do we obtain a threshold near the yellow–blue¹ line simply because the average chromaticity of our referents falls close to that line?

It is the case that individual referents were tested in separate blocks within the experimental runs of Experiment 1; and each separate block, terminated only after 15 reversals of the staircase, lasted several minutes – a time that should allow any adaptation to the brief stimulus probes to be re-set. Nevertheless, we have performed a control experiment in which we introduce strong biases into the sets of referents and show that the minimum is not displaced.

5. Experiment 2. Methods

5.1. Stimuli and procedures

For this control experiment, we chose a $+45^\circ$ line in a region where the monitor gamut allowed us to extend the referents well above and below the provisional ‘yellow–blue’ line of Fig. 1B. This

$+45^\circ$ line intersected the yellow–blue line at an $L/(L+M)$ coordinate of 0.64. We chose two subsets of 10 referents lying along this line, one biased to higher values of $L/(L+M)$, one to lower. A central set of six referents was common to the two subsets.

The two subsets were tested in independent, interleaved experimental runs. There were six independent repetitions of each condition, the first being discarded as practice. In six short runs interleaved with the threshold measurements, we also made estimates of the position of the red–green equilibrium hue for this $+45^\circ$ line. All other experimental procedures and stimulus conditions were as for Experiment 1.

5.2. Observers

There were four observers, two of them naïve as to the purposes of the experiment. Observers 1, 2 and 5 had completed Experiment 1; Observer 6 was a new male observer, a native French speaker. Testing was in Cambridge.

6. Experiment 2. Results

The results for this control experiment are shown in Fig. 4, where the ordinate is the factor by which the discriminanda differ from the referent at threshold, and the abscissa is the $L/(L+M)$ coordinate of the referent. Data for the high-bias and low-bias subsets are shown with different symbols. The vertical broken line in each panel shows our empirical estimate of the $L/(L+M)$ coordinate of the unique hue, as estimated from the phenomenological measurements that were interleaved with the performance measurements. The solid vertical line indicates the $L/(L+M)$ value of D65.

Bias in the referents does not appear to displace the position of the minimum thresholds. To confirm this, we performed a repeated-measures ANOVA for the six data points common to the high-bias and low-bias runs. The factors were: Observer, Bias (high or low) and referent ($L/(L+M)$ coordinate of the referent stimulus). There were significant effects of Observer ($F(3) = 50.5$; $p < 0.001$) and of referent ($F(5) = 7.35$, $p < 0.001$), but there was no effect of bias ($F(1) = .004$, $p = 0.95$). Thus it is very unlikely that the positions of minimal thresholds in Experiment 1 are the result of choosing sets of referents that are symmetrically placed around the provisional yellow–blue line.

Experiment 2 confirms the primary finding of Experiment 1: the minimal thresholds occur at a chromaticity close to the chromaticity that appears neither reddish nor greenish under the chosen conditions of adaptation. (See vertical broken lines for each observer in Fig. 4.) This chromaticity has a different $L/(L+M)$ coordinate from D65 (indicated by the solid vertical lines). Such a result would not be expected if discrimination depended strictly on the signals of a mid-ganglion cell system that extracted the ratio of long- and mid-wave cone excitations.

7. Experiment 3. Control for response errors

Is the variation in thresholds in Fig. 2 a truly sensory effect, or could it arise because the mapping between sensations – or their neural correlates – and responses is simple near the category boundary but is more ambiguous when, say, both the targets are saturated purples or saturated greens? The observer might see a difference between the half-fields but choose the wrong response.

We therefore performed a second control experiment in which the observer was asked only to detect a difference in chromaticity without reporting its direction. The stimulus field was divided into four quadrants (see inset, Fig. 5) and one of them, chosen at random on each trial, had a higher value of $L/(L+M)$. As before,

¹ For interpretation of color in Figs. 1–5, the reader is referred to the web version of this article.

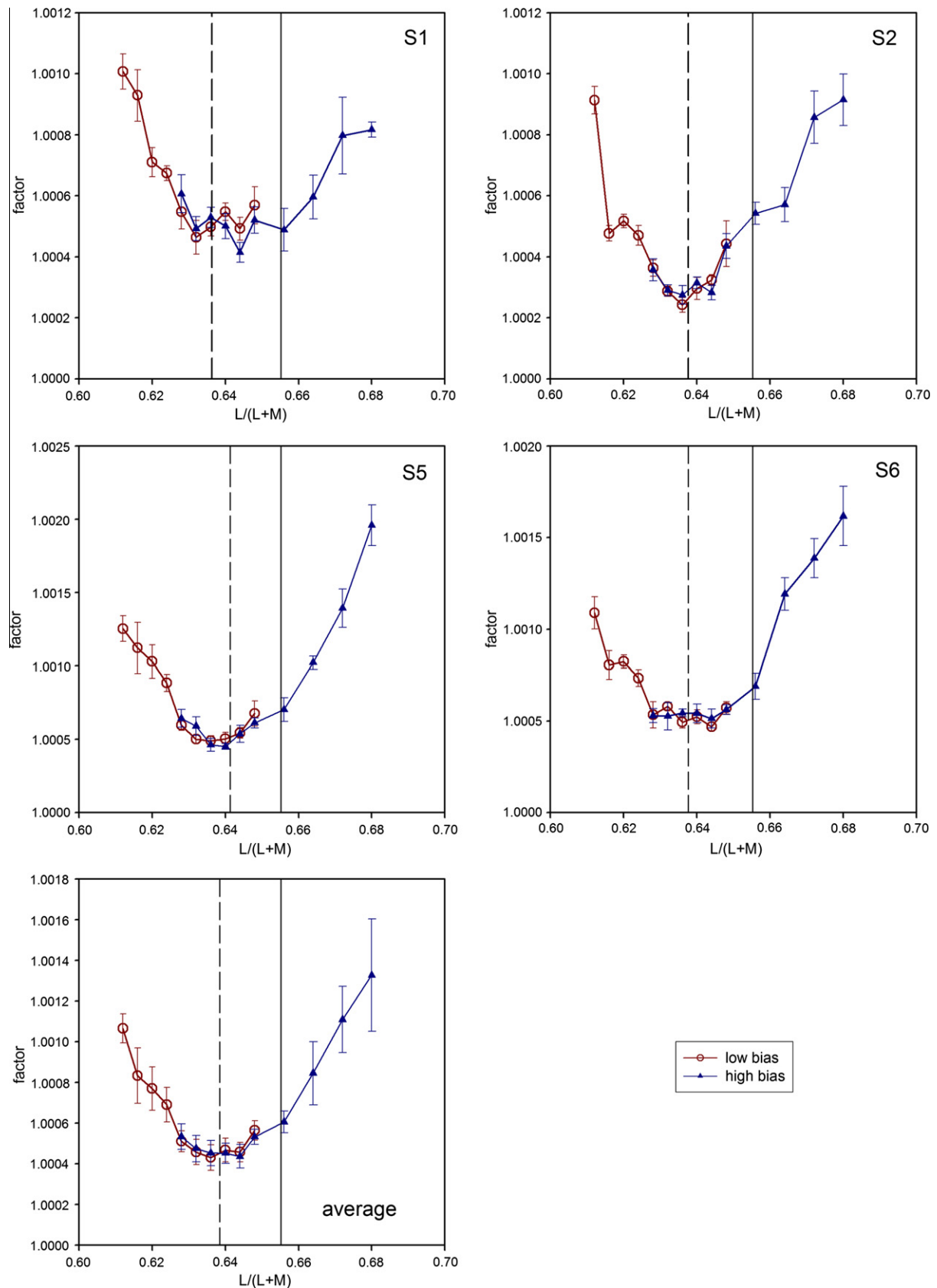


Fig. 4. Results for Experiment 2, in which the set of referent stimuli was biased either to low values of $L/(L+M)$ or to high values of $L/(L+M)$. The ordinate of each panel represents the factor by which each of the discriminanda differed from the referent at threshold. These thresholds are plotted against the $L/(L+M)$ coordinate of the referent. In the panels for individual observers, the error bars represent ± 1 SEM, based on five independent runs; for the average data, the error bars represent ± 1 SEM, based on the four means from independent observers. In each panel the vertical broken line shows the $L/(L+M)$ coordinate of the chromaticity that appeared neither reddish nor greenish under the conditions of adaptation used in the experiment: these lines coincide approximately with the minimum of threshold measurements. The solid vertical lines show the $L/(L+M)$ coordinate of the background (which was metameric to Illuminant D65): Note that these lines always lie to the right of the broken lines.

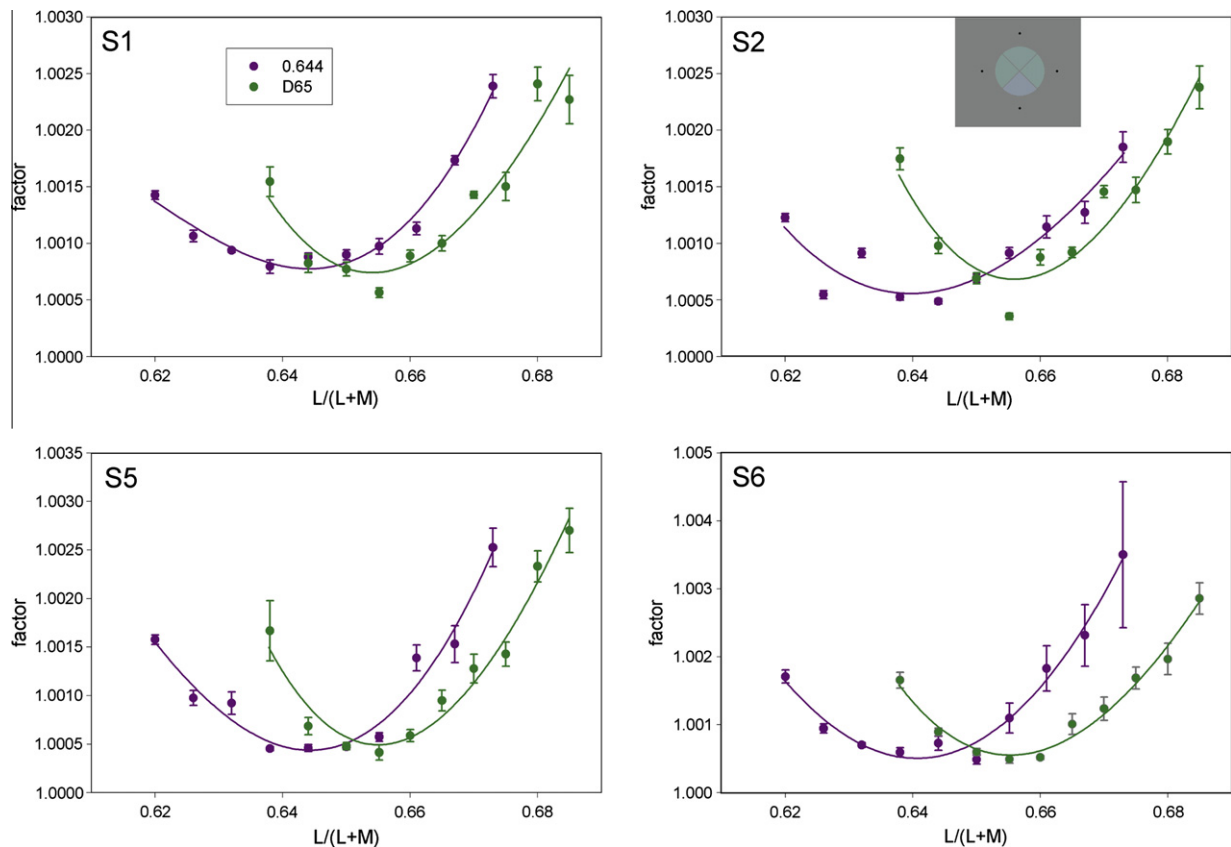


Fig. 5. Results of a control experiment in which the subject was asked only to identify the quadrant that differed in chromaticity from the other three. The stimulus arrangement is shown in the inset. For each observer, two data sets are shown corresponding to two of the $+45^\circ$ lines of Fig. 1B. The ordinate and abscissa are as for Fig. 2. Error bars represent ± 1 SEM, based on estimates from five independent experimental sessions. Note that the minima of the functions do not coincide with one another, contrary to the expectation if discrimination depended only on a neural channel that extracts the ratio of L and M cone excitations.

the variation in chromaticity was along a $+45^\circ$ line. The observer was now asked only to identify which of the four quadrants was the odd one.

8. Experiment 3: Methods

8.1. Stimuli and procedures

Thresholds were measured along two $+45^\circ$ lines, one passing through the metamer of D65 and one intersecting the provisional yellow–blue line at an $L/(L+M)$ coordinate value of 0.644 (second and third lines from the right in Fig. 1B). The target quadrant differed in chromaticity from the other quadrants along a $+45^\circ$ line and, as in Experiment 1, a staircase procedure was used to adjust the factor by which the target and distractor quadrants differed from the referent value. The two $+45^\circ$ lines were tested alternately, with six repetitions, the first pair being taken as practice. Other procedures and stimulus parameters were as for Experiment 1.

8.2. Observers

There were four observers, two of them naïve as to the purposes of the experiment. Observers 1 and 2 were the authors and were tested in St. Petersburg; observers 5 and 6 were tested in Cambridge.

9. Experiment 3: Results

The results of the control experiment are shown in Fig. 5. For the $+45^\circ$ line passing through D65, a strong minimum is found,

as before, close to the $L/(L+M)$ coordinate value of D65. However, for the second line, the minimum is firmly shifted to a lower $L/(L+M)$ value. This would not be expected if the discrimination depended on a chromatic channel that simply extracted the ratio of L and M signals.

Thus the phenomenon seen in Experiment 1, and earlier seen in our parafoveal measurements for spatially separated stimuli (Danilova & Mollon, 2010), is still present when the task is only to identify the odd quadrant in a centrally presented array. It becomes unlikely that the effect depends on color naming or on a reduction in response errors near the category boundary.

10. Discussion

Our performance measurements identify a locus in chromaticity space where discrimination thresholds are especially low. This furrow of low thresholds passes through the chromaticity of the neutral background, but it is not aligned with either of the cardinal axes of the chromaticity diagram. It is approximately coincident with the subjective boundary between reddish and greenish hues, a boundary that we independently estimated for our observers.

10.1. Minimal thresholds as a signature of a sensory channel in equilibrium

To interpret our results, we make one key assumption: The response function of a chromatic channel is steepest, and thus its differential sensitivity is greatest, at the equilibrium level set by the current background.

In the case of luminance contrast, differential sensitivity is almost invariably greatest at the luminance level to which the retina is adapted (Craik, 1938). At the physiological level, the response-vs.-intensity function of a visual channel is typically observed to shift so that its steepest part always corresponds with the current background level (Byzov & Kusnezova, 1971); and differential sensitivity will then be optimal when the discriminanda fall on this part of the response function.

De Valois, Abramov, and Mead (1967) found a similar result for color: Estimating wavelength discrimination for individual neurons in the macaque LGN, they showed that chromatically-opponent cells had a narrow response region of optimal sensitivity that was centered on the wavelength to which the cell was currently adapted. They note, for example, that before adaptation a ‘+R–G’ cell will give a response to 620-nm light that is virtually indistinguishable from its response to 630-nm light, since both these lights strongly excite the cell; but if the cell is allowed to adapt for a few seconds to 620-nm light, then the response will drop to close to the spontaneous level and the cell will readily signal a change to 630 nm. ‘Selective chromatic adaptation thus produces a loss of absolute wavelength information but leads to an increase in the discriminative power of the visual system.’

Several psychophysical studies of human color vision have shown a corresponding result: Discrimination is optimal for chromaticities close to that of the adapting background (Krauskopf & Gegenfurtner, 1992; Loomis & Berger, 1979; Miyahara, Smith, & Pokorny, 1993; Rautian & Solov’eva, 1954). And such a result is clearly seen in our own data: The lowest thresholds are obtained when the referent stimulus coincides with the chromaticity of the neutral background (which is metameric to Illuminant D65).

But the interest of the present results lies in what happens when the chromaticities of the probe stimuli depart from that of the adapting field. Suppose that discrimination depended on a midjet ganglion cell system that signals the ratio of excitation of the long- and middle-wave cones. For this dichromatic subsystem, there exist a set of tritan metamers – chromaticities that produce the same signal in the channel as does the background. These chromaticities lie on an approximately vertical line in the MacLeod–Boynton diagram; and it ought to be that thresholds are minimal near these chromaticities. Conversely, if discrimination were mediated by the other cardinal mechanism, which extracts the ratio $S/(L + M)$, then the minimal thresholds should be predicted by an approximately horizontal line in MacLeod–Boynton space, a line that passes through D65 and that represents a set of chromaticities for which S excitation is constant. In fact, the minimal thresholds lie along a line that passes obliquely through the chromaticity of D65. The depth of the minimum, however, declines with distance from D65.

10.2. A non-cardinal neural channel?

If we retain the principle that threshold minima are the signature of a sensory channel in equilibrium, our results suggest a chromatically opponent neural channel different from those conventionally assumed. This would be a channel that draws synergistic inputs from L and S cones and an opposed input from M cones.

Our psychophysical results cannot in themselves tell us the level at which the postulated channel emerges. Does it lie in parallel with those already reported in the early visual system or does it arise from a more central transformation of these early channels?

10.2.1. The parallel model

In recent electrophysiological studies, chromatically opponent neurons with non-cardinal tuning have been reported at the level of the LGN and cortical area V1, but most commonly the S -cone input is synergistic with the M -cone input (e.g. Conway, 2001; Hor-

witz, Chichilnisky, & Albright, 2006; Tailby, Solomon, & Lennie, 2008) and not with the L -cone input as our results would require. However, in classical electrophysiological studies of the retina and the lateral geniculate nucleus, there were occasional reports of opponent neurons in which L and S cone signals were synergistic (de Monasterio, Gouras, & Tolhurst, 1975; Valberg, Lee, & Tigwell, 1986); and such cells, though relatively uncommon in any one sample, have been reported in recent studies (e.g. Conway, 2001, Fig. 8; Horwitz, Chichilnisky, & Albright, 2006; Fig. 8; Tailby, Solomon, & Lennie, 2008, Fig. 3). In interpreting electrophysiological results, the absolute number of a given cell type may not be a secure guide: Factors such as cell size may bias the neurons that are recorded from; and central decisions in a particular task may well be based on the signals of a minority type of cell.

One reason for considering the possibility of an additional early channel is the discovery that the primate retina enjoys many more independent output channels than previously suspected (Dacey, 2004). A candidate substrate for an $L + S$ vs. M channel would be the large bistratified type of retinal ganglion cell, which is known to draw excitatory inputs from S cones (Dacey, 2003). Relevant here is the description of an 11th type of bipolar cell in Golgi-stained macaque retina (Dacey et al., 2011). These ‘giant’ bipolars avoid short-wave cones but contact long-wave or middle-wave cones. However, they contact only about half the cones within their dendritic field, suggesting that they are selective either for long-wave or for middle-wave cones. Such a bipolar cell would be well suited to supplying one of the inputs to a non-midget chromatic channel that drew signals of a particular sign only from long-wave cones or only from middle-wave cones.

Another retinal candidate for our channel would be a subtype of midget ganglion cell that drew inputs from S cones. Field et al. (2010), recording from peripheral retina of macaques, have reported that S -cone inputs to the center of the receptive field are frequent in the case of OFF-center midget ganglion cells and are also observed in a minority of ON-center cells.

10.2.2. The serial model

Alternatively, a red–green signal may be constructed by recombination of the cardinal peripheral channels at a more central, cortical stage – as has often been suggested in models of color vision (De Valois & De Valois, 1993). A serial model of this kind might account for our observation (see above, Fig. 2) that the very lowest thresholds are recorded only at the chromaticity of the background field (D65) and that the minimal thresholds become higher at points on the yellow–blue line more distant from the background chromaticity. The explanation would be that D65 is the only chromaticity at which both the second-stage (L vs. M) and the third-stage (‘red–green’) mechanisms are in the middle of their operating ranges.

10.3. Relationship to earlier work

Why has the present phenomenon not been observed in the many previous studies of color discrimination? The dominant tradition has been to measure ‘discrimination ellipses’, showing the thresholds for different directions of change about a fixed point in color space (MacAdam, 1942). The present effect would be observed only when the center of an ellipse fell close to the blue–yellow line. In fact, the existing literature does offer examples of ellipses that are oriented at approximately -45° in MacLeod–Boynton diagram, not only at the white point to which the observer is adapted (Beer, Dinca, & MacLeod, 2006; Boynton, Nagy, & Olson, 1983; Regan & Mollon, 1995), but also in the upper left and lower right quadrants of chromaticity space relative to the adaptation stimulus (Krauskopf & Gegenfurtner, 1992; their Fig. 14).

To reveal the present phenomenon, it is probably important that the differential sensitivity of the visual system should be probed briefly without changing the overall state of adaptation. In the classical era, when discrimination ellipses were measured, the eye would often be partly or fully adapted to the average chromaticity around which discrimination was being measured.

10.4. Enhanced discrimination at a category boundary

Independently of the possible physiological implications discussed above (Sections 10.1 and 10.2), the present results are of interest in themselves, in that they identify a locus of enhanced discrimination close to a subjective category boundary in human color space – the boundary between reddish and greenish hues. Our results show a considerable improvement in precision at the boundary, an improvement that survives when the task is reduced to one of identifying oddity. The effect is likely to be a truly sensory effect, rather than an enhancement that arises at a response stage.

The category boundary at which we find enhancement is not the type of boundary at which recent studies have commonly sought an enhancement. Most studies have concentrated on the boundary between two adjacent hues in the color circle, say, between blue and green. The present enhancement occurs at the center of a category, at or close to a unique hue – white, blue or yellow. The subject's task is one of discriminating between two binary hues, between, say, reddish blues and greenish blues. The enhancement of discrimination is most marked in the central region of the chromaticity diagram and is attenuated as the spectrum locus is approached; and we do not yet know whether thresholds are enhanced at other category boundaries.

The category boundary between reddish and greenish hues is a fundamental one for human perception. It may have universal ecological significance, since it coincides with the 'caerulean line', the locus of natural illuminants, mixtures of sunlight and skylight (Mollon, 2006). Moreover, a distinction between reddish and other colors is one that arises early in languages, immediately following terms for dark and light (Kay & Maffi, 1999).

If, however, the eye is adapted to a different chromaticity, the actual chromaticities that correspond to the subjective boundary between reddish and greenish hues are likely to be displaced (e.g. Smithson & Zaidi, 2004; Thornton & Pugh, 1983; Wei & Shevell, 1995). It is an interesting – and open – question whether the chromaticities of optimal discrimination will be displaced concomitantly.

Acknowledgments

Supported by Wellcome Trust Grant 082378/Z/07/Z, Royal Society International Exchanges Grant IE110252 and Russian Foundation for Basic Research Grant 12-04-01797-a.

References

- Beer, R. D., Dinca, A., & MacLeod, D. I. A. (2006). Ideal white can be yellowish or bluish, but not reddish or greenish (Abstract). *Journal of Vision*, 6(6), 417.
- Boynton, R. M., Nagy, A. L., & Olson, C. (1983). A flaw in equations for predicting chromatic differences. *Color Research and Application*, 8, 69–74.
- Burns, S. A., Elsner, A. E., Pokorny, J., & Smith, V. C. (1984). The Abney effect: Chromaticity coordinates of unique and other constant hues. *Vision Research*, 24, 479–489.
- Byzov, A. L., & Kusnezova, L. P. (1971). On the mechanisms of visual adaptation. *Vision Research Supplement*, 3, 51–63.
- Conway, B. R. (2001). Spatial structure of cone inputs to color cells in alert macaque primary visual cortex (V-1). *The Journal of Neuroscience*, 21, 2768–2783.
- Craik, K. J. W. (1938). The effect of adaptation on differential brightness discrimination. *Journal of Physiology (London)*, 92, 406–421.
- Dacey, D. M. (2003). Colour coding in the primate retina: Diverse cell types and cone-specific circuitry. *Current Opinion in Neurobiology*, 13, 421–427.
- Dacey, D. M. (2004). Origins of perception: Retinal ganglion cell diversity and the creation of parallel visual pathways. In M. S. Gazzaniga (Ed.), *The cognitive neurosciences* (pp. 281–301). Cambridge Mass: MIT.
- Dacey, D. M., Joo, H. R., Peterson, B. B., & Haun, T. J. (2011). Characterization of a novel large-field cone bipolar cell type in the primate retina: Evidence for selective cone connections. *Visual Neuroscience*, 28(1), 29–37.
- Dacey, D. M., & Lee, B. B. (1994). The 'blue-on' opponent pathway in primate retina originates from a distinct bistratified ganglion cell type. *Nature*, 367, 731–735.
- Danilova, M. V., & Mollon, J. D. (2010). Parafoveal color discrimination: A chromaticity locus of enhanced discrimination. *Journal of Vision*, 10(1), 4, 1–9.
- Danilova, M. V., & Mollon, J. D. (2003). Comparison at a distance. *Perception*, 32, 395–414.
- Danilova, M. V., & Mollon, J. D. (2006). The comparison of spatially separated colours. *Vision Research*, 46, 823–836.
- de Monasterio, F. M., Gouras, P., & Tolhurst, D. J. (1975). Trichromatic colour opponency in ganglion cells of the rhesus monkey retina. *Journal of Physiology*, 251, 197–216.
- De Valois, R. L., Abramov, I., & Mead, W. R. (1967). Single cell analysis of wavelength discrimination at the lateral geniculate nucleus in the macaque. *Journal of Neurophysiology*, 30, 415–433.
- De Valois, R. L., & De Valois, K. K. (1993). A multistage color model. *Vision Research*, 33(8), 1053–1065.
- DeMarco, P., Pokorny, J., & Smith, V. C. (1992). Full-spectrum cone sensitivity functions for X-chromosome-linked anomalous trichromats. *Journal of the Optical Society of America A*, 9, 1465–1476.
- Derrington, A. M., Krauskopf, J., & Lennie, P. (1984). Chromatic mechanisms in lateral geniculate nucleus of macaque. *Journal of Physiology*, 357, 241–265.
- Field, G. D., Gauthier, J. L., Sher, A., Greschner, M., Machado, T. A., Jepson, L. H., et al. (2010). Functional connectivity in the retina at the resolution of photoreceptors. *Nature*, 467(7316), 673–677.
- Franklin, A., Drivonikou, G. V., Clifford, A., Kay, P., Regier, T., & Davies, I. R. L. (2008). Lateralization of categorical perception of color changes with color term acquisition. *Proceedings of the National Academy of Sciences of the United States of America*, 105(47), 18221–18225.
- Gilbert, A. L., Regier, T., Kay, P., & Ivry, R. B. (2006). Whorf hypothesis is supported in the right visual field but not the left. *Proceedings of the National Academy of Sciences of the United States of America*, 103(2), 489–494.
- Gouras, P. (1968). Identification of cone mechanisms in monkey ganglion cells. *Journal of Physiology*, 199, 535–547.
- Hering, E. (1878). *Zur Lehre vom Lichtsinne. Sechs Mittheilungen an die Kaiserliche Akademie der Wissenschaften in Wien*. Wien: Carl Gerold's Sohn.
- Horwitz, G. D., Chichilnisky, E. J., & Albright, T. D. (2006). Cone inputs to simple and complex cells in V1 of awake macaque. *Journal of Neurophysiology*, 97, 3070–3081.
- Jordan, G., & Mollon, J. D. (1995). Rayleigh matches and unique green. *Vision Research*, 35(5), 613–620.
- Jordan, G., & Mollon, J. D. (1997). Unique hues in heterozygotes for protan and deutan deficiencies. *Colour Vision Deficiencies XIII*, 59, 67–76.
- Kay, P., & Maffi, L. (1999). Color appearance and the emergence and evolution of basic color lexicons. *American Anthropologist*, 101, 743–760.
- Krauskopf, J., & Gegenfurtner, K. (1992). Color discrimination and adaptation. *Vision Research*, 32(11), 2165–2175.
- Krauskopf, J., Williams, D. R., & Heeley, D. W. (1982). Cardinal directions of color space. *Vision Research*, 22(9), 1123–1131.
- Kuehni, R. G. (2004). Variability in unique hue selection: A surprising phenomenon. *Color Research and Application*, 29(2), 158–162.
- Lieberman, A. M., Harris, K. S., Hoffman, H. S., & Griffith, B. C. (1957). The discrimination of speech sounds within and across phoneme boundaries. *Journal of Experimental Psychology*, 54, 358–368.
- Loomis, J. M., & Berger, T. (1979). Effects of chromatic adaptation on color discrimination and color appearance. *Vision Research*, 19, 891–901.
- MacAdam, D. L. (1942). Visual sensitivities to color differences in daylight. *Journal of the Optical Society of America*, 32, 247–281.
- MacLeod, D. I. A., & Boynton, R. M. (1979). Chromaticity diagram showing cone excitation by stimuli of equal luminance. *Journal of the Optical Society of America*, 69, 1183–1186.
- Miyahara, E., Smith, V. C., & Pokorny, J. (1993). How surrounds affect chromaticity discrimination. *Journal of the Optical Society of America*, 10, 545–553.
- Mollon, J. D. (2006). Monge. *Visual Neuroscience*, 23, 297–309.
- Mollon, J. D. (2009). A neural basis for unique hues? *Current Biology*, 19, R441–R442.
- Mollon, J. D., & Jordan, G. (1997). On the nature of unique hues. In C. Dickinson, I. Murray, & D. Carden (Eds.), *John Dalton's colour vision legacy* (pp. 381–392). London: Taylor and Francis.
- Nerger, J. L., Volbrecht, V. J., & Ayde, C. J. (1995). Unique hue judgements as a function of test size in the fovea and at 20-deg temporal eccentricity. *JOSA A*, 12, 1225.
- Rautian, G. N., & Solov'eva, V. P. (1954). Vlijanie svetlogo okrugeniya na ostrotu cvetorazlocheniya. *Doklady Akademii Nauk SSSR*, 95, 513–515.

- Regan, B. C., & Mollon, J. D. (1995). Discrimination ellipses in the MacLeod–Boynton diagram: Results for normal and colour-deficient subjects obtained with a CRT display. In B. Drum (Ed.), *Colour vision deficiencies XII* (pp. 444–451). Dordrecht: Kluwer.
- Regan, B. C., Reffin, J. P., & Mollon, J. D. (1994). Luminance noise and the rapid determination of discrimination ellipses in colour deficiency. *Vision Research*, 34, 1279–1299.
- Roberson, D., Hanley, J. R., & Pak, H. (2009). Thresholds for color discrimination in English and Korean speakers. *Cognition*, 112, 482–487.
- Roberson, D., Pak, H., & Hanley, J. R. (2008). Categorical perception of colour in the left and right visual field is verbally mediated: Evidence from Korean. *Cognition*, 107, 752–762.
- Rushton, W. A. H. (1972). Pigments and signals in colour vision. *Journal of Physiology*, 220, 1P–31P.
- Shevell, S. K. (2003). Color appearance. In S. K. Shevell (Ed.), *The science of color* (pp. 149–190). Elsevier.
- Smith, V. C., & Pokorny, J. (1975). Spectral sensitivity of the foveal cone photopigments between 400 and 500 nm. *Vision Research*, 15, 161–171.
- Smith, V. C., & Pokorny, J. (2003). Color matching and color discrimination. In S. K. Shevell (Ed.), *The science of color* (pp. 103–148). Amsterdam: Elsevier.
- Smithson, H., & Zaidi, Q. (2004). Colour constancy in context: Roles for local adaptation and levels of reference. *Journal of Vision*, 4(9), 693–710.
- Sternheim, C. S., & Boynton, R. M. (1966). Uniqueness of perceived hues investigated with a continuous judgemental technique. *Journal of Experimental Psychology*, 72, 770–776.
- Stockman, A., & Sharpe, L. T. (2000). The spectral sensitivities of the middle- and long-wavelength-sensitive cones derived from measurements in observers of known genotype. *Vision Research*, 40, 1711–1737.
- Tailby, C., Solomon, S. G., & Lennie, P. (2008). Functional asymmetries in visual pathways carrying S-cone signals in macaque. *Journal of Neuroscience*, 28, 4078–4087.
- Thornton, J. E., & Pugh, E. N. Jr., (1983). Red/green color opponency at detection threshold. *Science*, 219(4581), 191–193.
- Valberg, A., Lee, B. B., & Tigwell, D. A. (1986). Neurones with strong inhibitory S-cone inputs in the macaque lateral geniculate nucleus. *Vision Research*, 26, 1061.
- Webster, M. A., Webster, S. M., Bharadwaj, S., Verma, R., Jaikumar, J., Madan, G., et al. (2002). Variations in normal color vision. III. Unique hues in Indian and United States observers. *Journal of the Optical Society of America A: Optics, Image Science, and Vision*, 19(10), 1951–1962.
- Wei, J., & Shevell, S. K. (1995). Color appearance under chromatic adaptation varied along theoretically significant axes in color space. *Journal of the Optical Society of America A: Optics, Image Science, and Vision*, 12(1), 36–46.
- Wetherill, G. B., & Levitt, H. (1965). Sequential estimation of points on a psychometric function. *British Journal of Mathematical and Statistical Psychology*, 18, 1–10.
- Winawer, J., Witthoft, N., Frank, M. C., Wu, L., Wade, A. R., & Boroditsky, L. (2007). Russian blues reveal effects of language on color discrimination. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 7780–7785.
- Witzel, C., Hansen, T., & Gegenfurtner, K. R. (2009). Categorical reaction times for equally discriminable colours. *Perception*, 38, 14.
- Wyszecki, G., & Stiles, W. S. (1982). *Color science*. New York: Wiley.
- Zhou, K., Mo, L., Kay, P., Kwok, V. P. Y., Ip, T. N. M., & Tan, L. H. (2010). Newly trained lexical categories produce lateralized categorical perception of color. *Proceedings of the National Academy of Sciences of the United States of America*, 107(22), 9974–9978.